Geology

The oldest Pinus and its preservation by fire

--Manuscript Draft--

Manuscript Number:	G37526R2
Full Title:	The oldest Pinus and its preservation by fire
Short Title:	The oldest Pinus and its preservation by fire
Article Type:	Article
Keywords:	Pinaceae; fire; charcoal; evolution; molecular phylogeny
Corresponding Author:	Howard James Falcon-Lang, PhD Royal Holloway, University of London Egham, Surrey UNITED KINGDOM
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Royal Holloway, University of London
Corresponding Author's Secondary Institution:	
First Author:	Howard James Falcon-Lang, PhD
First Author Secondary Information:	
Order of Authors:	Howard James Falcon-Lang, PhD
	Viola Mages
	Margaret Collinson
Order of Authors Secondary Information:	
Manuscript Region of Origin:	CANADA
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Response to Reviewers:	

Publisher: GSA
Journal: GEOL: Geology
DOI:10.1130/G37526.1

The oldest *Pinus* and its preservation by fire

Howard J. Falcon-Lang, Viola Mages, and Margaret Collinson

Department of Earth Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK

ABSTRACT

Pinus (Pinaceae) is a diverse conifer genus that dominates Northern Hemisphere forests today, and is noteworthy for its fire-adapted traits. Here we describe the oldest known fossils attributable to the genus from the Lower Cretaceous (Valanginian, ~133–140 Ma) part of the Chaswood Formation of Nova Scotia, Canada. *Pinus mundayi* sp. nov. comprises charred long-shoots, which show a constellation of derived characters including (1) axial resin ducts with thin-walled epithelial cells in the secondary xylem and phloem, (2) fenestriform or pinoid cross-field pits, and (3) helically-arranged short-shoots that pass through growth ring boundaries before distally diverging into two separate needle bases. The fossils, which are interpreted as remains of an evergreen 2-needle pine, provide a new constraint on timetrees of Pinaceae evolution. Their preservation as charcoal and the occurrence of resin ducts, which produce flammable terpenes in modern pines, show that *Pinus* has co-occurred with fire since its Mesozoic origin.

INTRODUCTION

The Pinaceae is the most diverse and widespread family of conifers, comprising 11 genera and c. 230 species (Eckenwalder, 2009). It dominates large areas of the Northern Hemisphere, especially in cool temperate and taiga biomes (Farjon, 2010), a biogeographic pattern established in Early Cretaceous time (Peralta-Medina and Falcon-

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DOI:10.1130/G37526.1

Lang, 2012). A sister taxon to all other crown-group conifers, molecular studies suggest that stem-Pinaceae diverged in Late Triassic time (Lu et al., 2014) with the origin of the most diverse Pinoideae crown-group (*Pinus*, *Picea*, and *Cathaya*; Gernandt et al., 2011) delayed until Late Jurassic time (Lin et al., 2010). However, accurate calibration of such timetrees is limited by the paucity of well-dated fossils, with the first representative of non-pinoid crown-group conifers (Podocarpaceae) known from Late Triassic time, the first stem-Pinaceae known from Late Jurassic time (Rothwell et al., 2012), and the oldest fossils attributable to extant pinoid genera occurring in Early Cretaceous time (Ryberg et al., 2012; Klymiuk and Stockey, 2012).

The evolutionary history of *Pinus* has attracted special interest because, not only is it the most diverse (~115 species) genus of Pinaceae (Farjon, 2010), but also it exhibits fire-adapted ecological traits (Keely, 2012). These are restricted to *P.* subgenus *Pinus*, in which there are two end-member fire strategies: (1) *fire-tolerators* rapidly grow to great height, utilize thick bark, and self-prune lower branches, to maximize resilience to low-intensity surface fires; (2) *fire-embracers* store flammable deadwood, to promote lethal crown fires, but deploy fire-dependent serotinous cones, to ensure post-fire cohort-renewal (Keely, 2012). Molecular studies suggest that these adaptations arose in Early Cretaceous time (He et al., 2012) when atmospheric oxygen levels were elevated (Glasspool and Scott, 2010) and fires were common (Brown et al., 2012). However, Early Cretaceous fossil evidence for *Pinus* being part of a fire-prone community is lacking.

In this paper, we describe the oldest known fossils referable to *Pinus*, and emphasize their preservation as charcoal, the product of wildfire (McParland et al., 2007).

Findings extend the antiquity of this genus, provide a new constraint for molecular timetrees, and demonstrate that *Pinus* has co-occurred with fire since its Mesozoic origin.

GEOLOGICAL CONTEXT

The *Pinus* fossils were obtained from Bailey Quarry, near Windsor, Nova Scotia, Canada (45°01′10′′N; 64°03′31′′W). At this site, deposits of the 'lower member' of the Cretaceous Chaswood Formation unconformably infill hollows in the weathered top of a gypsum unit assigned to the Carboniferous Windsor Group. The Cretaceous beds comprise pebbly sandstone units showing low-angle cross-stratification and trough cross-bedding, interpreted as the deposits of braided rivers that flowed through 'tower karst' topography. These fluvial deposits contain charred mesofossils as concentrated lag deposits and also yield an associated palynoflora of conifers (including many bisaccate forms), ginkgos, bennettites, cycads, ferns and lycopsids (Falcon-Lang et al., 2007).

The palynoflora contains *Aequitriradites verrucosus*, *Distaltriangulisporites perplexus* and *Trilobosporites canadensis* indicating a Cretaceous (Valanginian–Hauterivian) age compared with North American sections (Burden and Hills, 1989). Based on the Last Appearance Datum of *T. canadensis* that determination can be refined to an early Valanginian age compared to more proximal sites within the Atlantic Rift (Taugourdeau-Lantz, 1988). This placement is consistent with the diversity of *Cicatricosisporites* spore types, which suggests proximity to the Jurassic–Cretaceous boundary (Abbink et al., 2001). A younger age is unlikely because *Plicatella* spores are rare (one specimen found), *Appendicisporites* spores are absent, and angiosperm pollen is also lacking. Younger Barremian palynofloras at this paleolatitude (30 – 40ºN) typically

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DOI:10.1130/G37526.1

show greater abundance and diversity of *Plicatella* and *Appendicisporites* species (Burden and Hills, 1989) and contain angiosperm pollen (Heimhofer et al., 2005).

METHODS

Bulk samples were digested in 40% HF to release charcoal, and the residue washed in distilled water. Charred conifer axes (up to 20 mm long) were fixed to aluminum stubs using Electrodag 550 (nickel acrylic colloid), coated in 150 Å of gold palladium using an ISI Sputter coater and viewed at 15 kv with a Hitachi S-3500N Scanning Electron Microscope. The exterior of each specimen was imaged before being removed from the stub, dissected with a scalpel under a binocular microscope, and remounted in order to image internal anatomy. Half of each specimen was retained intact, while the other half was fractured and imaged along transverse (TS), radial longitudinal (RLS), and tangential longitudinal (TLS) surfaces to allow direct comparison with illustrations in the literature. When compared with extant conifer material, measurements were corrected to account for charring-induced contraction using published coefficients (Falcon-Lang et al., 2012).

CHARRED *PINUS* MESOFOSSILS

The *Pinus* fossils show features indicative of preservation as charcoal, the product of wildfire, such as homogenization of adjacent tracheid cell walls, elevated reflectance, and fire-cracks (McParland et al., 2007). Fossils are described as a new species.

Pinus mundayi sp. nov., Falcon-Lang, Mages, Collinson (Fig. 1)

Diagnosis: Eustelic long shoots with endarch primary xylem patches, axial resin ducts with 6 – 10 thin-walled epithelial cells in both the secondary xylem and phloem, fenestriform or pinoid cross-field pits, and helically-arranged short-shoots (3/8

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DOI:10.1130/G37526.1

phyllotaxic fraction) that pass through growth ring boundaries and distally diverge as two separate needle bases; ray tracheids are absent.

Holotype and repository: NSM016GF004.001, Nova Scotia Museum, Halifax, Canada

Other material: NSM016GF004.002–004.

Locality: Bailey Quarry, near Windsor, Nova Scotia, Canada

Stratigraphy and age: Chaswood Formation (Cretaceous, Valanginian)

Etymology: epithet in honor of Derek and Mary Munday of Bodowen, Barmouth

Description of Long-Shoots

Long-shoots, 3.6–4.2 mm diameter and <17 mm long, preserve the pith, primary vasculature, secondary xylem, and (locally) phloem (Fig. 1A–B). The stellate pith, 1.15 mm diameter (Fig. 1B), is composed of axially-elongate parenchyma, cells 100–120 µm high and 20–25 µm diameter, with profuse pits on all walls. The eustele comprises ~20 endarch primary xylem patches (Fig. 1C), composed of scalariform tracheids, ~10 µm diameter. The secondary xylem, 1.2–1.4 mm in radius, comprises one or two rings of growth, each ring being composed of thin-walled earlywood tracheids, 10–25 µm diameter, that pass centripetally into thick-walled latewood, 10–15 µm diameter. Earlywood tracheids show 1–2-seriate, circular, bordered pits, 10–15 µm, with circular apertures (Fig. 1M), and opposite arrangement where biseriate. Latewood tracheids lack pits or show sparse, circular bordered pits only. Rays are uniseriate, 1–11 cells high (Fig. 1K), and lack ray tracheids. Cross-fields of ray parenchyma show 1–4 fenestriform or pinoid pits (Fig. 1N). A few scattered axial parenchyma strands also occur close to axial resin ducts. A thin layer of secondary phloem, <350 µm radius (Fig. 1I), locally adheres to the outermost part of the shoot; periderm is not preserved.

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Description of Short-Shoot Bases

Prominent short-shoot bases, 0.7–1.1 mm diameter, are helically arranged on the preserved exterior of the long-shoot with a 3/8 phyllotaxic fraction (Fig. 1A). In cross-section, short-shoot bases are oval in the proximal part of their course, comprising a pith and a concentric xylem cylinder (Fig. 1L). More distally, they diverge into two separate kidney-shaped bundles of secondary xylem that represent needle bases (Fig. 1H). In more mature specimens (NSM016GF004.004), traced from the pith, short-shoots pass through one or two subtle growth ring boundaries in the secondary xylem (Fig. 1D).

Description of Resin Ducts

Resin ducts occur within the secondary xylem and phloem of long-shoots. In the secondary xylem, axial resin ducts, 60–90 µm diameter, locally tylose-filled, and surrounded by 6–10 epithelial cells, are common in the earlywood (Fig. 1C, E) but reduce in frequency and size (30 µm diameter) toward the latewood. Radial resin ducts, 40–50 µm diameter, with 6–8 epithelial cells (Fig. 1J) are present in some fusiform rays with a density of 2.6 per mm^2 (based on limited observations of small areas). In the phloem, axial resin ducts, 40 µm diameter, occur (Fig. 1I). Resin ducts also occur within short-shoot bases, where typically 1–4 axial ducts, 40–110 µm diameter, with 6–9 epithelial cells, occur (Fig. 1L). In all cases, epithelial cells are thin-walled, a characteristic that can be ascertained by comparing half the double-wall width of fused tracheid cell walls with those of epithelial cells (Fig. 1F). Epithelial cell walls lack pits except where in contact with vasicentric axial parenchyma.

Diagnostic Characters of *Pinus* Seen in Fossils

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A noteworthy character of the long-shoots is the presence of resin ducts (Fig. 1C). Where axial ducts occur in secondary xylem, wood anatomists distinguish schizogenously formed 'normal' ducts (tubular, and generally solitary) from 'traumatic' ducts (cyst-like and typically in tangential series) triggered by environmental shock (Lin et al., 2002). Although traumatic ducts occur in the secondary xylem of several of the eight families of the Pinales, especially in Cupressaceae and Pinaceae (Cleary and Holmes, 2011), normal axial ducts, as seen in the Bailey Quarry long-shoots, are confined to five genera of Pinaceae: *Pinus*, *Picea*, *Cathaya*, *Larix*, and *Pseudotsuga* (Wu and Hu 1997). Normal ducts occasionally occur in the secondary xylem of *Nothotsuga* (Lin et al., 1995) and *Keteeleria* (Lin et al., 2000), but they are absent from juvenile shoots so those genera are unlike the fossils.

The wall thickness of epithelial cells that surround 'normal' axial ducts in the secondary xylem (Fig. 1F) is a further key feature for fossil diagnosis (Wu and Hu, 1997). *Pinus* shows thin-walled (unlignified) epithelial cells that are thinner than the walls of adjacent tracheids, whereas the other Pinaceae genera have thick-walled (lignified) epithelial cells similar to tracheids (Lin et al., 2002). This distinction is not completely clear-cut because 9% of the ~115 extant *Pinus* species have thick-walled epithelial cells (Esteban et al., 2004) and some juvenile *Picea* shoots show of a mixture of thin- and thick-walled epithelial cells (Lin et al., 2002). Applying this criterion, the long-shoots from Bailey Quarry, which show exclusively thin-walled epithelial cells, are probably *Pinus*, although referral to *Picea* cannot be completely excluded based on these characters alone because the fossil material is juvenile.

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However, other anatomical characters collectively confirm placement of the fossils in *Pinus* and rule out other possible taxa with resin ducts as follows:

(1) Axial resin ducts occur in the secondary phloem (Fig. 1I), a feature that is never seen in *Cathaya*, *Picea* or *Pseudotsuga* but is typical of *Larix* and *Pinus* (Lin et al., 2002);

(2) Axial resin duct diameter is always >60 µm (after correction; Fig. 1E), a feature characteristic of almost all *Pinus* species, but absent elsewhere in Pinaceae (Esteban et al., 2004);

(3) Radial duct density is ~1.3 per mm^2 (after correction), a value that is within the normal range for *Pinus* (0.5 – 2), but uncharacteristic of *Cathaya* (0.7), *Larix* (0.15 – 0.7), *Picea* (0.3 – 0.4), or *Pseudotsuga* (0.15 – 0.2) (Lin et al., 2002);

(4) Cross-field pits are fenestriform or pinoid (Fig. 1N), typical of *Pinus* but uncharacteristic of the piceoid pits of *Pseudotsuga*, *Larix*, *Picea*, and *Cathaya* (Esteban et al., 2004) even when distortion due to charring is taken into account (Gerards et al. 2007); and

(5) Divergent secondary xylem bundles in the more distal course of short-shoots suggest they bore two needles per fascicule (Fig. 1H; Dörken et al., 2010), a feature that is strongly suggestive of *Pinus* because other Pinaceae (with the exception of *Larix*) bear single leaves directly attached to main shoots (Farjon, 2010).

DISCUSSION

Based on anatomical analysis, *Pinus mundayi* sp. nov., reported here, is the oldest known representative of the genus (~133–140 Ma; Valanginian). *Pinus yorkshirensis*, the former oldest recognizable member of the genus, is based on material of uncertain provenance, but palynology of attached sediment indicates an origin in rocks close to the

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Hauterivian–Barremian (~129 Ma) boundary (Ryberg et al., 2012). The new fossils therefore extend the record of *Pinus* by 4–11 myrs, meaning that it is of similar antiquity to the oldest known *Picea*, which is also of Valanginian age (Klymiuk and Stockey, 2012). Although pinaceous cones of *Pityostrobus*-type are abundant from Barremian time onward (~129 Ma), their systematic position within the Pinaceae is poorly resolved (Rothwell et al., 2012). The new fossils are therefore only one of three pre-Albian occurrences identifiable to an extant genus of Pinaceae, and improve calibration of molecular timetrees of the family (Lin et al., 2010). In addition, the occurrence of two needles per fascicle suggests an affinity with *Pinus* subgenus *Pinus* (Farjon, 2010) and implies that subgeneric diversification may have occurred earlier than previously thought (Gernandt et al., 2011). Further, based on its unusual short-shoot/long-shoot syndrome, it has been hypothesized that ancestral *Pinus* was deciduous (Dörken et al., 2010); however, the passage of short-shoots through > 2 growth rings demonstrates that the fossil short-shoots were evergreen as seen in extant species.

The preservation of long-shoots as charcoal, also, may be significant. Fire-adaptive traits are widespread within *Pinus*, and especially in *P.* subgenus *Pinus* (Keely, 2012), an ecology that is hypothesised to have originated in Early Cretaceous time based on molecular clock estimates (He et al., 2012). However, testing of this hypothesis is hampered by the fact that neither *Pinus* nor securely identified Pinaceae have hitherto been identified in Cretaceous charcoal assemblages (Brown et al., 2012). While our charred long-shoot fossils show, for the first time, that *Pinus* burned in Early Cretaceous fires, and probably, crown fires, this does not prove fire-adaption as all plants occasionally burn. Crown fires are characteristic of fire-embracer pines (Keely, 2000),

but the fossils lack evidence, such as serotinous cones, to demonstrate adaption. The only fossil feature that is noteworthy is the occurrence of axial resin ducts. In extant *Pinus*, these ducts secrete terpene, a highly flammable, unsaturated hydrocarbon that contributes to fire ecology (He et al., 2012). Therefore, the occurrence of resin ducts and preservation as charcoal in *P. mundayi* are consistent with He et al. (2012)'s hypothesis that fire-adaptive traits of *Pinus* originated in Early Cretaceous time, but do not provide confirmation.

ACKNOWLEDGMENTS

HFL acknowledges a NERC Advanced Postdoctoral Fellowship (NE/F014120/2). The comments of Andrew Leslie, two other anonymous reviewers, and the editor, greatly improved this paper.

REFERENCES CITED

Abbink, O.A., Callomon, J.H., Riding, J.B., Williams, P.D.B., and Wolfard, A., 2001, Biostratigraphy of Jurassic-Cretaceous boundary strata in the Terschelling Basin, The Netherlands: Proceedings of the Yorkshire Geological Society, v. 53, p. 275–302, doi:10.1144/pygs.53.4.275.

Brown, S.A.E., Scott, A.C., Glasspool, I.J., and Collinson, M.E., 2012, Cretaceous wildfires and their impact on the Earth System: Cretaceous Research, v. 36, p. 162–190, doi:10.1016/j.cretres.2012.02.008.

Burden, E.T., and Hills, L.V., 1989, Illustrated key to genera of Lower Cretaceous terrestrial palynomorphs (excluding megaspores) of western Canada: American Association of Stratigraphic Palynologists, Contributions Series, no. 21, 147 p.

Cleary, M.R., and Holmes, T., 2011, Formation of traumatic resin ducts in the phloem of western redcedar (*Thuja plicata*) roots following abiotic injury and pathogenic invasion by *Armillaria ostoyae*: The International Association of Wood Anatomists Journal, v. 32, p. 351–359.

Dörken, V.M., Stephan, G., and Stützel, G., 2010, Morphology and anatomy of anomalous short shoots in *Pinus* (Pinaceae) and their evolutionary meaning: Feddes Repertorium, v. 121, p. 133–155, doi:10.1002/fedr.201000006.

Eckenwalder, J.E., 2009, Conifers of the World: Portland, Oregon, Timber Press, 720 p.

Esteban, L.G., Palacios, P.P., Casasús, A.G., and Fernández, F.G., 2004, Characterization of the xylem of 352 conifers: Investigación Agraria: Sistemas y Recursos Forestales, v. 13, p. 452–478.

Falcon-Lang, H.J., Fensome, R.A., Gibling, M.R., Malcom, J., Fletscher, K.R., and Holleman, M., 2007, Karst-related outliers of the Cretaceous Chaswood Formation of Maritime Canada: Canadian Journal of Earth Sciences, v. 44, p. 619–642, doi:10.1139/e06-119.

Falcon-Lang, H., Wheeler, E.A., Baas, P., and Herendeen, P.H., 2012, A diverse charcoalified assemblage of Cretaceous (Santonian) angiosperm woods from Upatoi Creek, Georgia, U.S.A. Part 1. Morphotypes with scalariform perforation plates: Review of Palaeobotany and Palynology, v. 184, p. 49–73, doi:10.1016/j.revpalbo.2012.03.016.

Farjon, A., 2010, A Handbook of the World's Conifers: Leiden, Brill Academic Publishers, 1112 p, doi:10.1163/9789047430629.

Gerards, T., Damblon, F., Wautho, B., and Gerrienne, P., 2007, Comparison of cross-field pitting in fresh, dried and charcoalified softwoods: The International Association of Wood Anatomists Journal, v. 28, p. 49–60.

Gernandt, D.S., León-Gómez, C., Hernández-León, S., and Olson, M.E., 2011, *Pinus nelsonii* and a cladistic analysis of Pinaceae ovulate cone characters: Systematic Botany, v. 36, p. 583–594, doi:10.1600/036364411X583565.

Glasspool, I.J., and Scott, A.C., 2010, Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal: Nature Geoscience, v. 3, p. 627–630, doi:10.1038/ngeo923.

He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W., and Lamont, B.B., 2012, Fire-adapted traits of Pinus arose in the fiery Cretaceous: The New Phytologist, v. 194, p. 751–759, doi:10.1111/j.1469-8137.2012.04079.x.

Heimhofer, U., Hochuli, P.A., Burla, S., Dinis, J.M.L., and Weissert, H., 2005, Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change: Geology, v. 33, p. 141–144, doi:10.1130/G21053.1.

Keely, J.E., 2012, Ecology and evolution of pine histories: Annals of Forest Science, v. 69, 445–453, doi:10.1007/s13595-012-0201-8.

Klymiuk, A.A., and Stockey, R.A., 2012, A Lower Cretaceous (Valanginian) seed cone provides the earliest fossil record for *Picea* (Pinaceae): American Journal of Botany, v. 99, p. 1069–1082, doi:10.3732/ajb.1100568.

Lin, C.-P., Huang, J.-P., Wu, C.-S., Hsu, C.-Y., and Chaw, S.-M., 2010, Comparative chloroplast genomics reveals the evolution of Pinaceae genera and subfamilies: Genome Biology and Evolution, v. 2, p. 504–517, doi:10.1093/gbe/evq036.

Lin, J.X., Hu, Y.S., and Wang, F.H., 1995, Wood and bark anatomy of Nothotsuga (Pinaceae): Annals of the Missouri Botanical Garden, v. 82, p. 603–609, doi:10.2307/2399841.

Lin, J., Lin, E., and Farjon, A., 2000, The occurrence of vertical resin canals in *Keteleeria*, with reference to its systematic position in Pinaceae: Botanical Journal of the Linnean Society, v. 134, p. 567–574, doi:10.1111/j.1095-8339.2000.tb00552.x.

Lin, J., Hu, Y., He, Y., and Ceulemans, R., 2002, Systematic survey of resin canals in Pinaceae: Belgian Journal of Botany, v. 135, p. 3–14.

Lu, Y., Ran, J.-H., Guo, D.-M., Yang, Z.-Y., and Wang, X.-Q., 2014, Phylogeny and divergence times of gymnosperms inferred from Single-Copy Nuclear Genes: PLoS One, v. 9, p. e107679, doi:10.1371/journal.pone.0107679.

McParland, L., Collinson, M.E., Scott, A.C., Steart, D.C., Grassineau, N.V., and Gibbons, S.J., 2007, Ferns and fires: Experimental charring of ferns compared to wood and implications for paleobiology, paleoecology, coal petrology and isotope geochemistry: Palaios, v. 22, p. 528–538, doi:10.2110/palo.2005.p05-138r.

Peralta-Medina, E., and Falcon-Lang, H.J., 2012, Cretaceous forest composition and productivity inferred from a global fossil wood database: Geology, v. 40, p. 219–222, doi:10.1130/G32733.1.

Rothwell, G.R., Mapes, G., Stockey, R.A., and Hilton, J., 2012, The seed cone *Eathiestrobus* gen. nov.: Fossil evidence for a Jurassic origin of Pinaceae: American Journal of Botany, v. 99, p. 708–720, doi:10.3732/ajb.1100595.

Ryberg, P.E., Stockey, R.A., Hilton, J., Mapes, G., Riding, J.B., and Rothwell, G.W., 2012, Reconsidering relationships among stem and crown group Pinaceae: Oldest

record of the genus *Pinus* from the Early Cretaceous of Yorkshire, UK: International Journal of Plant Sciences, v. 173, p. 917–932, doi:10.1086/667228.

Taugourdeau-Lantz, J., 1988, Stratigraphic implications of Early Cretaceous spores and pollen grains at holes 638B, 638C, and 641C, Leg 103, off the Iberian Margin, eastern North Atlantic: Proceedings of the Ocean Drilling Program, Scientific Results, v. 103, p. 419–429.

Wu, H., and Hu, Z.-H., 1997, Comparative anatomy of resin ducts in the Pinaceae: Trees (Berlin), v. 11, p. 135–143, doi:10.1007/s004680050069.

FIGURE CAPTIONS

Figure 1. *Pinus mundayi* (all images of holotype, NSM016GF004.001, except D, NSM016GF004.004) from the Cretaceous (Valanginian) of Nova Scotia, Canada. A., Lateral view of long-shoot showing helically arranged short-shoot bases (ss), and prominent fire cracks (fc); scale: 2 mm. B., Cross-section of long-shoot showing stellate pith (pi), short-shoot traces (sst), secondary xylem (sx) and fire-cracks (fc); TS, scale: 400 µm. C., Detail from (B) showing pith (pi), endarch primary xylem patches (arrows), short shoot traces (sst), and axial resin ducts (ard, arrow); TS, scale: 150 µm. D., Growth ring boundary (grb) in secondary xylem (sx); TS, scale: 250 µm. E., Cross section of an axial resin duct (ard) and its epithelial cells (ec) in secondary xylem (sx); TS, scale: 30 µm. F., Detail from (D) showing thin-walled epithelial cells (ec) of an axial resin duct (ard). Adjacent cells include thin-walled parenchyma (p) and thick-walled tracheids (tr) for comparison, also note absence of wall layering in tracheid cell walls, a characteristic

of charcoal; TS, scale: 15 µm. G., Longitudinal section of axial resin duct (ard) in secondary xylem (sx); RLS, scale: 100 µm. H., Cross-section through distal part of short shoot base showing diverging secondary xylem bundles (sx) of two needle bases, and fire-cracks (fc); TS, scale: 250 µm. I., Outer edge of secondary xylem (sx) and phloem (ph) containing an axial resin duct (ard, arrow); TS, scale: 75 µm. J., Radial resin duct (rrd) with epithelial cells (ec) within fusiform ray (fr); epithelial cells are thin-walled but coated with a volatile residue; oblique TLS, scale: 25 µm. K., Short, uniseriate rays in the secondary xylem close to the pith; TLS, scale: 75 µm. L., Cross-section through proximal part of short shoot base showing pith (pi) and concentric secondary xylem (sx) cylinder with axial resin ducts (ard, arrow); TS, scale: 250 µm. M., Circular, uniseriate, bordered pits in secondary xylem; RLS, scale: 25 µm. N., Fenestriform to pinoid cross-field pitting in secondary xylem; RLS, scale: 50 µm.

[1]GSA Data Repository item 2016xxx, xxxxxxxx (Phylogeny teaching slide and justification of new species), is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

Figure 1

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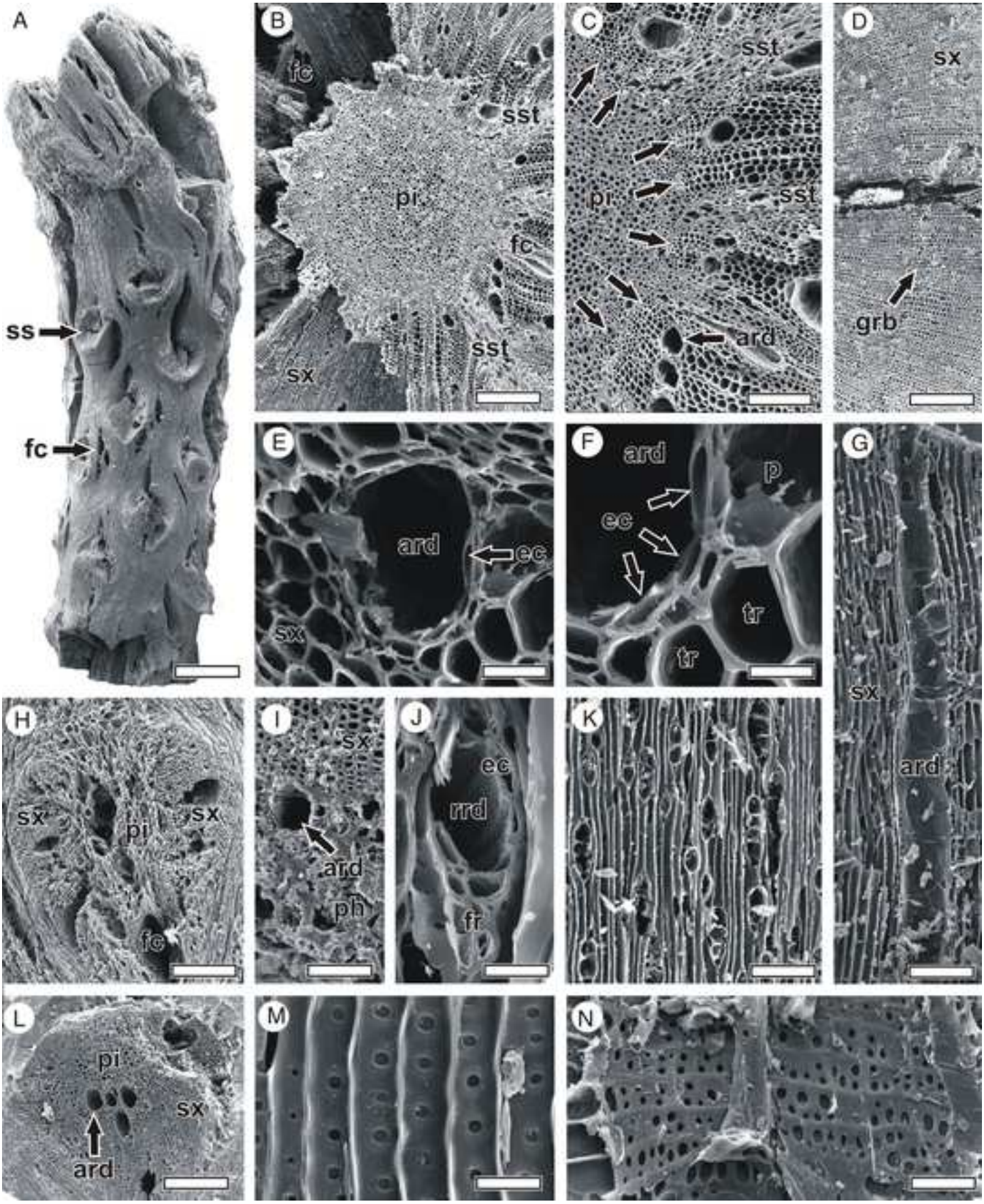
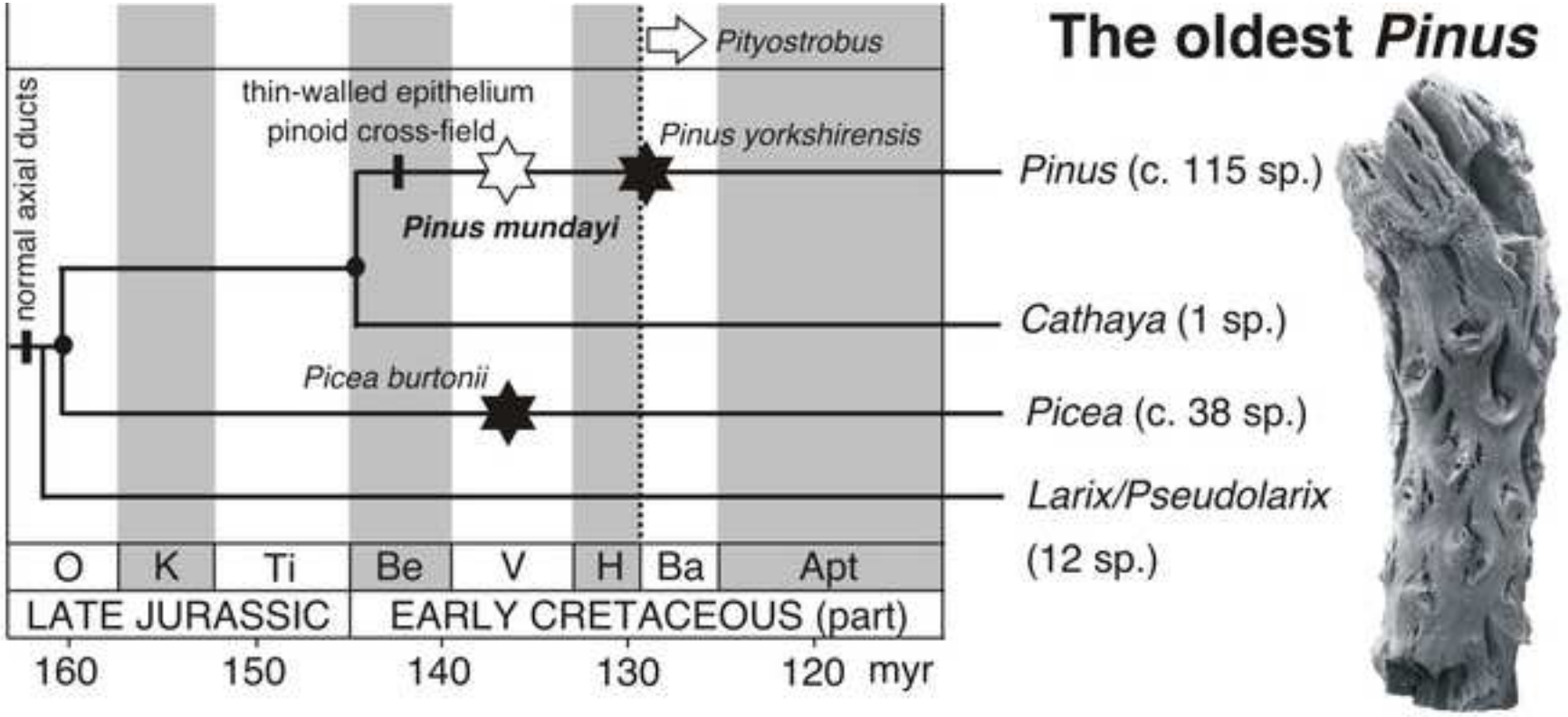
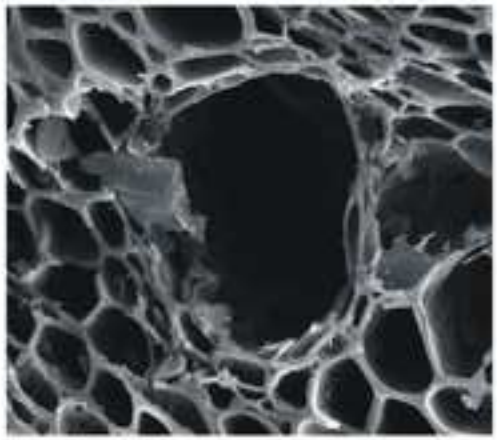
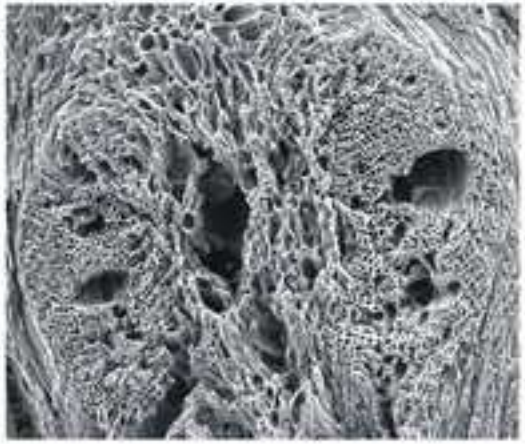


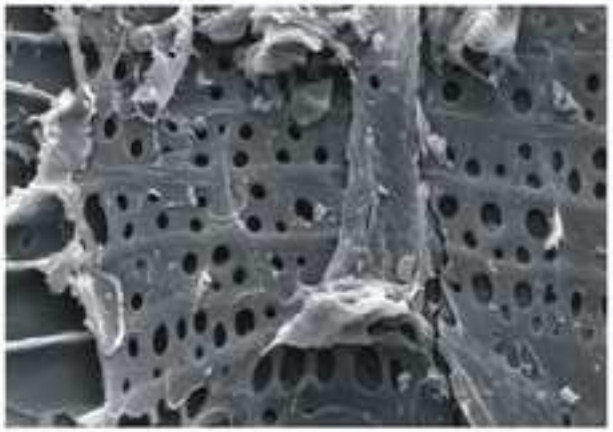




axial resin ducts with thin-walled epithelial cells

short-shoots that separate into two needle bases





pinoid and fenestriform cross-field pits

Falcon-Lang et al. 2016. The oldest Pinus and its preservation by fire. Geology, v. 44, p. xxx-xxx.

Supplementary discussion: Justification for a new species

Plant fossils are usually preserved in a disarticulated state, and new taxa are described based on individual organs; there are very few taxa reconstructed as 'whole-plants'. The new *Pinus* fossils described here comprise remains of partial twigs, with short shoot bases, lacking fertile remains. We note that there is a paucity of anatomically-preserved pinaceous twigs in the Cretaeous fossil record. Prior to this paper, the oldest described twig material is from the Cretaceous (Cenomanian) of the Czech Republic, some 40 million years younger than our new *Pinus* fossils; however, that material is assigned to family level only, and all other Cretaceous fossils that are similar to modern pines are based on secondary xylem only, and therefore assigned to genera such as *Pinuxylon* (Peralta-Medina and Falcon-Lang, 2012) rather than *Pinus sensu stricto*. Based on the antiquity, rarity, good preservation, and genus-level identification of the new material, it is advantageous to apply a binomial name, to allow its discussion in the literature.

As the material is assignable to the extant genus, *Pinus*, it is also necessary to consider how the fossil differs from the c. 115 extant species. *Pinus* is subdivided into two subgenera, *Pinus* Pinus and *Pinus* Strobus (Farjon, 2010). *Pinus* subgenus Strobus shows, typically, five needles per fascicle, whereas *Pinus* subgenus Pinus, shows, variably, 1 to 8 needles per fascicle (Farjon 2010). Our new *Pinus* fossils consistently show two needles per fascicle suggesting an affinity with *Pinus* subgenus Pinus (Farjon, 2010), and implying that the two subgenera diverged earlier than previously thought (Gernandt et al., 2011).

In *Pinus* subgenus Pinus, the number of needles per fascicle is species-specific in the range of (1) 2 – 5 (8) needles per fascicle (Farjon 2010). Two needles per fascicle is a stable characteristic of the 19 species of so-called 'Old World Pines' only: *P. densata, P. densiflora, P. hawnshanensis, P. kesiya, P. latteri, P. luchuensis, P. massoniana, P. merkusii, P. mugo, P. nigra, P. resinosa, P. sylvestris, P. tabuliformis, P. taiwanensis, P. thunbergii, P. tropicalis, P. uncinata, and P. yannanensis* (Farjon, 2010). A few additional species may show two needles per fascicle but in these taxa, the number of needles per fascicle is highly variable (1-5), unlike the stable two needle state observed in our material (Farjon, 2010).

Another important character state of the new *Pinus* fossils is their 3/8 phyllotaxic fraction. The most common phyllotaxic fractions in *Pinus* subgenus Pinus approximate to 1/3, 2/5, 3/8, and 5/13 (Farjon, 2010). Of the classic 'Old World Pines' that show two needles per fascicle, the most common fractions are 2/5 and 5/13 (Farjon, 2010). Only *P. sylvestris* and *P. nigra* has a phyllotaxic fraction that commonly and closely approximates to 3/8 (i.e., 135^{o}) (Farjon, 2010). According to the analysis of the wood of 352 conifer species compiled by Esteban et al. (2004), the new fossil *Pinus* differs from *P. sylvestris* and *P. nigra*, and most other 'Old World Pines' based on the absence of alternate ray tracheids. Therefore, the fossil material can justifiably be treated as a new species.